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THE LIFE OF A CALIFORNIAN POPULATION OF THE FACULTATIVE MILKWEED BUG, *LYGAEUS KALMII* (HETEROPTERA: LYGAEIDAE)

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Abstract.—*Lygaeus kalmii* is bivoltine in Monterey County, California. A major portion of the spring generation develops at sites distant from milkweeds; these nymphs feed on insect carrion as well as the seeds of *Lepidium nitidum* (Cruciferae) and other forbs. Cohorts reared in the absence of milkweeds survive well and produce viable offspring. The adults of the spring generation undertake dispersal flights during the late morning and afternoon on sunny days. Following dispersal, these adults are closely associated with *Asclepias eriocarpa*, a host that they can apparently locate by using olfactory cues. Milkweed seeds do not become available until several weeks after the spring adults disperse; the bugs do not copulate during the first part of this interval. The large populations of adults that move to *A. eriocarpa* during June and July can do considerable damage to the plants. These voracious adults also scavenge the numerous insects that are trapped in the milkweed pollinia, cannibalize each other, and, interestingly, attack the pupae of the monarch butterfly, *Danaus plexippus*, and the egg masses of the milkweed beetle, *Chrysochus cobaltinus*. The second generation feeds heavily on milkweed seeds. The reduviid, *Rhynocoris ventralis*, is a predator of adult *L. kalmii*.

Lygaeus kalmii Stål is a conspicuous bug that is commonly encountered in stands of milkweeds (*Asclepias* spp.) throughout much of North America (Slater and Knop, 1969). Our knowledge of this species has accumulated in a manner that is considered exemplary by scientific philosophers. Following the early descriptive work by Townsend (1887) and Simanton and Andre (1936) on life history, research has focused on the detailed, more carefully controlled examination of particular aspects of the biology, e.g. Caldwell's (1974) work on dispersal behavior and Evans' (1983) studies of the factors influencing host selection. Simultaneously, observers have amended and corrected the original descriptions as new details came to light (e.g. Dingle and Caldwell, 1971; Price and Willson, 1979). During this process, the species has been shown to display considerable geographic variation in morphology (Slater and Knop, 1969) and recent reports (Hunt, 1979; Slater, 1983; Wheeler, 1983) demonstrate that host requirements are less restricted than previously assumed. Data from collections and the literature lead one to suspect that there is interesting regional variation in phenology, food habits, and dispersal behavior. Our understanding of *L. kalmii* has thus reached a stage where it is useful to examine the life of a local population on the basis of these new insights.

My aim in this paper is to describe the niche of *L. kalmii* in Monterey County, California, and to report field observations on aspects of its biology that have been studied chiefly in the laboratory. To provide an account that is coherent, yet brief, I will comment on published results from other populations only in those cases where the comparison or verification is of particular interest. Readers seeking a complete bibliography on this species can consult Slater (1964, 1983), Evans (1983), and Wheeler (1983).

Environment

My observations focused on a *Lygaeus kalmii* population that inhabited a large tract of land (ca. 500 ha) at the Hastings Natural History Reservation in the Coast Range, Monterey County, California. This locality has mild, wet winters and hot, dry summers; conditions during my major period of study (Fig. 1) were normal for the region. The vegetation on the study area (490–820 m elevation) forms a complex mosaic of broadleaf evergreen forest (moist slopes), chaparral (dry slopes), and deciduous oak woodlands (Griffin, 1974).

All of the *Lygaeus* I found were in open woodlands and long-abandoned hayfields that had been established by merely removing a few trees from oak "savannas" (White, 1966). The herbaceous layer in these habitats is dominated by annual grasses and forbs that set seed and dry in late spring. *Asclepias eriocarpa* Benth., the only prevalent milkweed on the study area, occurs in these same, open habitats. These plants were distributed in 19 isolated stands that contained from 10–200 ramets. In addition, there was a large stand, which I will refer to as the "Arnold Field," of several hundred ramets scattered over an area of ca. 8 ha. Based on the recollections of residents and old notes, it is likely that many of these stands are at least 40 years old and that some may be much older. *Asclepias eriocarpa* is a large perennial that remains succulent throughout the summer.

Procedures

I studied the populations at the Hastings Reservation in 1975 (17 April–21 July, 20–23 October), 1976 (11–19 August), and 1983 (1–4 August). My general approach was that of a naturalist. I went out almost daily to observe and take notes in the field; these activities served to continuously raise and refine questions that were answered by further observations and simple experiments. Similar observations made on *Lygaeus* species in Colombia, Colorado, Missouri, and New York helped me to place this Californian population in perspective.

The adults in two milkweed stands, as well as some of the bugs that were observed in experimental cages, were given individual marks by placing tiny dabs of rapid-drying enamel on the pronotum and corium. Marked bugs were observed to fly at least 30 m and to survive at least 21 days in the field.

The densities of *L. kalmii* and other arthropods on milkweeds were measured as follows. While walking along a predetermined direction across a milkweed stand, I stopped every seventh stride and, with my eyes closed, pointed to a spot to my right and about 3 m away. The milkweed stem growing most closely to this spot was circled slowly and all of the large, active insects were counted. A beating sheet was then placed beside the stem, which was cut at its base and searched carefully. All of the insects on the stem (or surrogates for any that were observed to escape) were placed in a vial of ethanol. The ground around the base

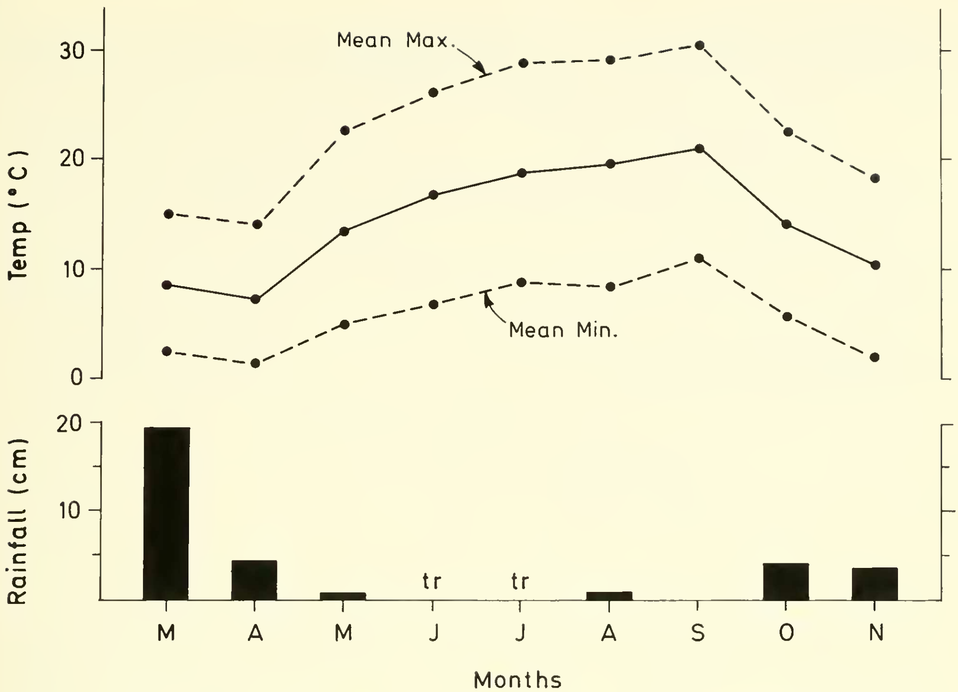

Fig. 1. Weather conditions at the Hastings Reservation during 1975. The weather station is located near the lower end of the study area at 545 m elevation. The extreme temperatures during this year were −7°C in January and 41°C in July. "tr" indicates a trace of precipitation.

of the stem was next searched for insects known to feed commonly on milkweeds. The aboveground plant parts were separated into foliage, inflorescences, pods, and stems; these were later dried and weighed. Each sample consisted of at least 50 stems collected in this manner.

I employed a variety of special censuses and simple experiments to examine particular aspects of behavior. These will be described with the results.

Field results were supplemented by observations on bugs reared in petri plates and assorted small jars. All cages had large openings, covered by dacron mesh, for ventilation. The bugs always had access to water which they obtained by probing absorbent cotton in vials that were filled with spring water. The cages were kept outdoors in a location where they were under light shade from mid-morning to late afternoon. The bugs were transferred to a clean cage about every 10 days. Since rearing conditions were uncontrolled, I did not measure developmental rate, clutch size, or other population parameters that were likely to depend on temperature and humidity.

I identified all of the insect species mentioned in the text. Voucher specimens, labelled "Lot 1120," have been placed in the Cornell University Insect Collection. James R. Griffin checked all of the plant identifications.

Seasonal Cycle and Habitat Use

Adult *L. kalmii* have been found overwintering in woodrat houses at the Hastings Reservation (Linsdale and Tevis, 1951). When my observations began in

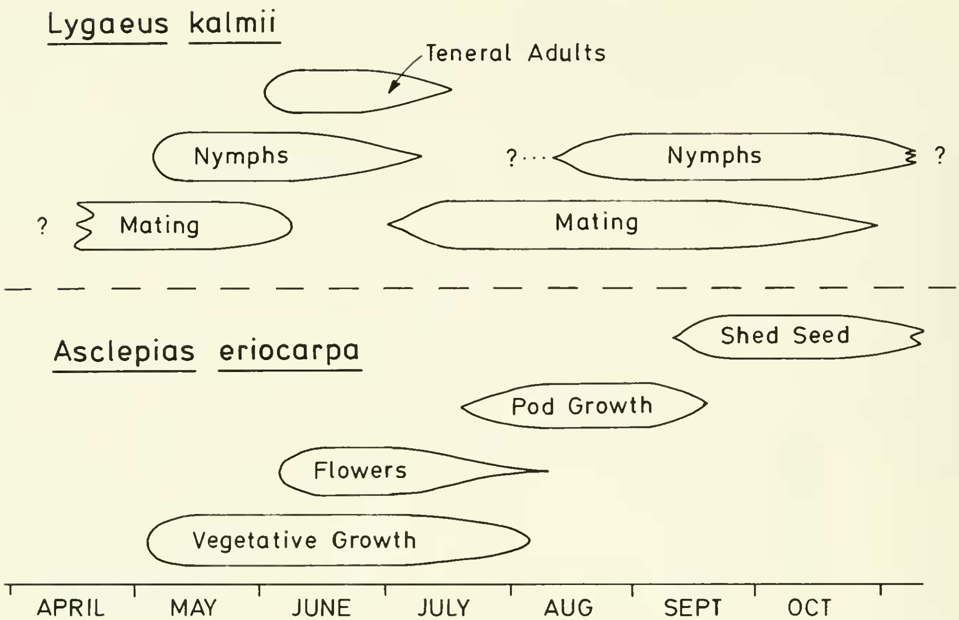

Fig. 2. Approximate phenology of *Lygaeus kalmii* and *Asclepias eriocarpa* at the Hastings Reservation, Monterey County, California. ? indicates occurrences that were inferred rather than directly observed.

mid-April, adults were already foraging in the open and copulating. The species is thus active well before the green shoots of milkweeds, *Asclepias eriocarpa,* poke above ground in early May (Fig. 2). Small aggregations, containing nearly equal proportions of both sexes, were found at this season near dried milkweed stalks that were produced the previous year. No milkweed seeds were found on the ground in most of these stands even though I made a concerted search for them. Furthermore, several aggregations occurred at locations at least 100 m from a milkweed stand. On 9–12 May 1975, I marked the bugs that had gathered within a 5 m^2 area, away from milkweeds, along a dirt lane. The density varied from 15 to 25 adults during this period. Three males remained on the area for at least four days. Since the sex ratio of newly marked bugs was about equal and males were recaptured more frequently (6 of 7 recaptures on 12 May and 5 of 5 on 14 May), it seems likely that the females tend to leave such aggregations relatively quickly.

During April and May the bugs were localized in open areas where individuals could easily move between patches of bare soil and herbaceous cover. Diggings by fossorial mammals and the edges of dirt roadways often provided these conditions. At this season the bugs foraged and mated chiefly on the ground. When it was cool and sunny, they spent much of the time running about where the sun had warmed the soil; when the ground was hot and after sunset, they tended to retreat to sheltered locations such as down cracks in the soil or under the basal rosettes of forbs.

I observed a female lay a large, but sterile, clutch of eggs in the field on 21 April. The earliest viable clutches, however, were not found until 12 May. The oviposition sites I discovered in the field included the hollow stems of dried forbs, the crevices between the appressed, terminal leaves of milkweeds, and the exposed surface of a fallen leaf. In the cages, females oviposited in the hollow stems of forbs (the diameter of the cavity had to be large enough that they could insert the terminal portion of the abdomen), in wads of absorbent cotton, and under excised leaves.

On 15 and 16 May, I located several groups of first and second instar nymphs. Some nymphs were present in the milkweed stands, but the bulk of this new spring generation was located in favorable sites away from milkweeds. These sites presented a mosaic of bare soil and herbaceous vegetation and usually contained an assortment of weedy forbs. While such areas are often associated with disturbance, they nonetheless form a large portion of the natural, ungrazed grassland at the Hastings Reservation because of the extensive activities of pocket gophers, *Thomomys bottae.* I studied young nymphs by marching across the grassland, throwing down a tarpaulin as I approached a likely looking area, and then carefully searching around its edges. I frequently encountered densities of 5^+ nymphs/m^2 at locations over 40 m from the nearest milkweed. Early instars were usually discovered under basal rosettes of forbs or moving along the ground in spots where sparse vegetation provided partial shade.

During May, the intact carcasses of dead adults were frequently encountered in the milkweed stands and on the margins of bare patches in the open grassland. Some of the overwintered generation of adults persisted, and continued to copulate, until mid-June.

Development of the nymphs proceeded rapidly during May and the first teneral adults appeared during the first week of June. At this time, the annual plants that dominate the herbaceous vegetation were becoming quite dry; the milkweeds, however, were succulent and just beginning to bloom. It seems clear that the spring generation can complete development well away from milkweeds. For instance, on 14 June I found late instar nymphs at seven of nine sites that were located in grassland at least 30 m from the nearest milkweed stem (I had not searched previously for bugs at these stations). On this date, I swept fifth instar nymphs from the grass at three other locations over 150 m from the nearest milkweed. Older nymphs were present in milkweed stands but their densities appeared to be comparable with those encountered in the open grassland. Almost all of the spring generation had completed development by 19 July.

Following dispersal (described below), the new generation of adults was closely associated with milkweeds. These adults spent much time up on plants where they fed heavily on flowers and buds. Between 15 June and 3 July, no copulation was seen among the thousands of adults that I encountered. Less than 0.1% of a huge population that I observed on 4 July were mating. In mid-July, when copulating pairs were regularly seen, the succulent milkweeds in the most vigorous stands were just beginning to initiate pods. All of the plants in the less vigorous stands began to yellow at this time; several stands that were heavily used by *L. kalmii* in June and early July did not produce any seed pods during either 1975 or 1976.

My knowledge of *L. kalmii* at the Hastings Reservation during the remainder of the year is based on my observations in October 1975 and August 1976 and 1983, and by notes made, at my request, by John Davis, James R. Griffin, and Walter Koenig. Despite the onset of copulation in July, we were unable to find nymphs of the summer generation until 17 August when a few scattered first and second instars were found on milkweeds. At this time, the plants had pods that were nearly mature size, but none of these had opened yet.

In late summer, adults continued to copulate and forage on milkweeds and on the ground nearby. Adults were often found below ground, in the spaces between the milkweed stalks growing from the same root crown and in recent diggings by pocket gophers. While a few adults continued to lurk around the dried out milkweed stands, the bulk of the population was concentrated in vigorous stands with maturing pods. No adults or nymphs were found away from milkweeds in the types of habitats that were used so extensively in the spring.

Milkweed pods began to open in mid-September; the shedding of new seeds continued through October. In late October 1976, after the onset of the autumn frosts and rains, adults and nymphs (including some in the second instar) were still concentrated in the vigorous milkweed stands where they often foraged on the ground. A few adults were copulating in late October. W. Koenig (personal communication) found active nymphs and adults out as late as 20 November and 12 December 1976, respectively.

Food Habits

The appearance of adults before milkweeds emerge and the occurrence of both nymphs and adults at great distances from milkweeds indicate that *L. kalmii* can reproduce and develop by using other resources. To determine what these alternative foods might be, I carefully observed (often with a 4× magnifier) feeding bugs, noting where the stylets were inserted and the effort required to extract the mouthparts after the bug was disturbed. In addition to probing the stems and leaves of milkweeds, the overwintered adults were seen to feed on insect "carrion" (e.g. *Eleodes* beetles that had been struck by a car) and on the developing seeds of *Erodium cicutarium* (Geraniaceae). Caged adults were observed repeatedly to feed on carcasses of grasshoppers and of other milkweed bugs and to cannibalize freshly laid eggs. Twice I observed caged adults attacking and piercing conspecific adults that had been moving sluggishly. In another instance, a female, which had been brought in from the field the previous day, thrice pursued and attempted to pierce a teneral adult before she encountered and killed another adult that was lame.

The basal rosettes and crevices that provide shelter for the nymphs in spring also act to accumulate seeds and debris (including insect carcasses) that are blown or washed across patches of bare soil. In such situations, early instars often fed on the seeds of *Lepidium nitidum* (Cruciferae) and another, unidentified forb. Later instars also utilized the seeds of *Calandrinia ciliata* (Portulacaceae). Caged nymphs were seen to feed on dead grasshoppers and engage in various acts of cannibalism; first instar nymphs ate eggs and third instar nymphs impaled soft, freshly molted nymphs. In Napa County, California, K. Evans (personal communication) found nymphs feeding and developing on the seeds of a composite, probably *Achyrachaena mollis*.

The *L. kalmii* population can certainly subsist and develop in spring and early summer without access to milkweeds. Two overwintered females, taken from the field on 23 April, were caged with mates and maintained on a diet of dead grasshoppers, seeds of *Calandrinia ciliata* and *Lepidium nitidum*, and water. One of these females lived until 13 June and laid three clutches that each contained 12–34 viable eggs; the other lived until 8 July and laid four clutches that each contained 20–40 eggs. Three of these clutches were reared on the same diet given their parents; each of these produced several adults, which proved capable of mating and laying viable eggs without ever tasting a milkweed. The absence of milkweeds from the diet of a variable portion of the individuals in a population may help to account for the high variation in the cardenolide content of *L. kalmii* collected at different localities and seasons (Isman et al., 1977).

The adults of the spring generation fed voraciously after arriving in the milkweed stands. During June and July, they tended to concentrate on the inflorescences where they often probed flower buds and peduncles. When feeding on mature flowers, they tended to insert their mouthparts in the column (which covers the pollinia), rather than the hoods (which secrete nectar). Ants, *Crematogaster* sp., that were harvesting nectar sometimes displaced bugs from mature flowers by nipping at their beaks. Adult *L. kalmii* also fed from the major veins of leaves and on the tips of certain leaves where their repeated feeding (marked by wounds scabbed over by latex) caused yellowing.

During summer, adults frequently fed on insect tissues. The copious nectar produced by *A. eriocarpa* attracted abundant insects, many of which were trapped when their legs became jammed in the slits of pollinia and could not be withdrawn (Woodson, 1954, describes pollination in *Asclepias* spp.). Dead honeybees that had been ensnared in this manner were frequently scavenged by *L. kalmii.* On one occasion I observed adults feeding on honeybee carcasses lodged beneath a reduviid (*Apiomermis* sp.) that was ambushing pollinators at a milkweed inflorescence. Clusters of adults were also found feeding on dead ants, adult *L. kalmii,* and adults of the milkweed-feeding chrysomelid, *Chrysochus cobaltinus* LeConte. In light of the extensive literature on aposematism and the ecological chemistry of milkweed herbivores, it is interesting that *L. kalmii* is a predator on the immobile stages of other insects that feed on *Asclepias* spp. In the field, I observed five instances of adults feeding on the pupae of the monarch butterfly, *Danaus plexippus* Linnaeus, and one case in which two adults were feeding on a *D. plexippus* caterpillar (1 cm long) that was freshly killed. When leaves bearing clutches of *Chrysochus cobaltinus* eggs were introduced into a cage, an adult *L. kalmii* readily probed through the fecal case that was plastered over them and killed the eggs.

The pods of *A. eriocarpa* have thick, air-filled walls. As shown by Ralph (1976), such pods effectively protect the developing seeds from milkweed bugs. As a result, only a tiny portion of the milkweed seeds were available to *L. kalmii* until after mid-September. Prior to that time, the adults that fed on pods usually concentrated on the suture near the equator (see Ralph, 1976, for full description) and on small, aborted pods with walls damaged by chewing insects. Similarly, most of the nymphs that I found in August 1976 were associated with stems bearing pods in which the developing seeds had been partially exposed by gnawing insects. The exit holes left by pod-boring weevils, *Rhyssomatus* sp., frequently provide *L. kalmii* with access to developing seeds in Kansas, Minnesota, and New York (E. W. Evans and R. B. Root, unpublished observations). To simulate the damage observed at the Hastings Reservation, I clipped the tips off four scattered pods on 15 August 1976; when I returned on 17 August, each pod had

1–4 adults on it, and when I returned again on 19 August, each had 2–12 adults. Such heavy utilization of a resource made available by another herbivore illustrates the subtle interdependencies that can influence the structure of a plant-arthropod association.

An activity census that I made in a vigorous milkweed stand on the afternoon of 17 August 1976 gives an indication of how *L. kalmii* utilizes resources in summer. In this census, I walked across the stand and at every fifth stride, recorded the activity of every *L. kalmii* on the nearest milkweed stem and on the ground beneath it. Proceeding in this manner, I found 120 living adults (including 14 mating pairs), 8 dead adults, and no nymphs. Among the living, 66 were on milkweeds bearing pods, 40 were on milkweeds without pods, and 14 were on the ground or dried grasses. Of the 45 bugs that had their stylets inserted, 17 were feeding on pods, 15 on stems, 11 on leaves, 2 on dried flowers, 1 on a fallen dead leaf, and 1 on a *Danaus* pupa.

During the autumn, the bugs fed heavily on milkweed seeds, especially on those that had fallen to the ground. While some seeds were wafted far by the wind, most remained close to the parent plants. Often the down of individual seeds became matted together, producing wads of seeds that fell nearby. Even seeds with fluffy down that were shed individually usually travelled only a few meters.

Dispersal and Host Location

Over most of the season adults flew infrequently and for distances of only a few meters. During late June and early July, however, when the adults of the spring generation entered the population, there was an obvious increase in flight activity. At this time hardened adults readily took flight when approached and teneral adults often basked, head upward, on the tips of tall grasses where they appeared to be readying themselves for launch. On two occasions I watched bugs flying along a relatively straight course, 2 to 4 m above the ground; in both cases the bugs covered at least 30 m before I lost sight of them. Some adults, however, can remain quite sedentary during this period. Thus, three adults, first marked on 13 June, were recaptured in almost the same location on 4 July; of course, these individuals could have undertaken a dispersal flight prior to their first capture.

Table 1. Conditions on days when dispersing *L. kalmii* adults were collected on the surface of a swimming pool. The weather instruments were placed 150 m from the pool; temperature was measured with a recording thermometer in an instrument shelter and sunshine was measured with a Campbell Stokes recorder.

Date	Total Catch of *L. kalmii*	Maximum Temperature (°C)	Duration of Sunshine (min)
14 June	15	30	700
15	17	24	706
18	1	20	672
19	1	17	262
20	31	24	712
21	28	26	708
3 July	2	20	670
6	12	29	668
7	12	29	668

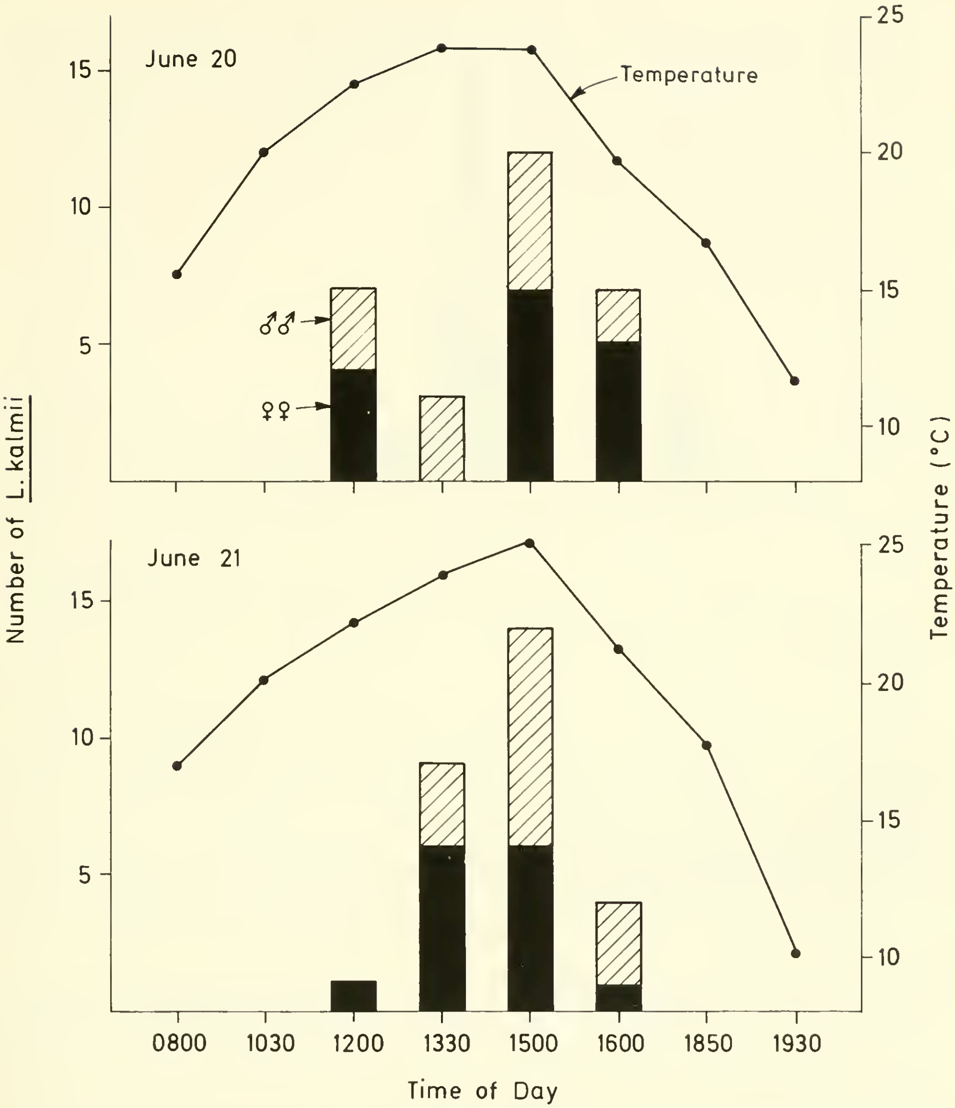

Fig. 3. Numbers of adult *L. kalmii* alighting in a swimming pool at different times of day. Temperatures were measured in an instrument screen. On both days, the sky was cloudless following the dissipation of morning fog prior to 0800.

Many of my observations on dispersal were made at a plastic swimming pool that was located 80 m from the nearest milkweed. I visited this pool, which had sides 125 cm high and a surface area of ca. 28 m^2, at intervals throughout the day and skimmed off all of the bugs that had dropped in since my previous visit. Bugs were first noticed in the pool on 13 June 1975. The largest collections were made on warm, sunny days (Table 1). Both sexes disperse and, judging from the alighting times, dispersal flights are undertaken chiefly during the late morning and afternoon (Fig. 3). No bugs were found in the pool on 13–21 July 1975, even though the weather was warm and clear during this period.

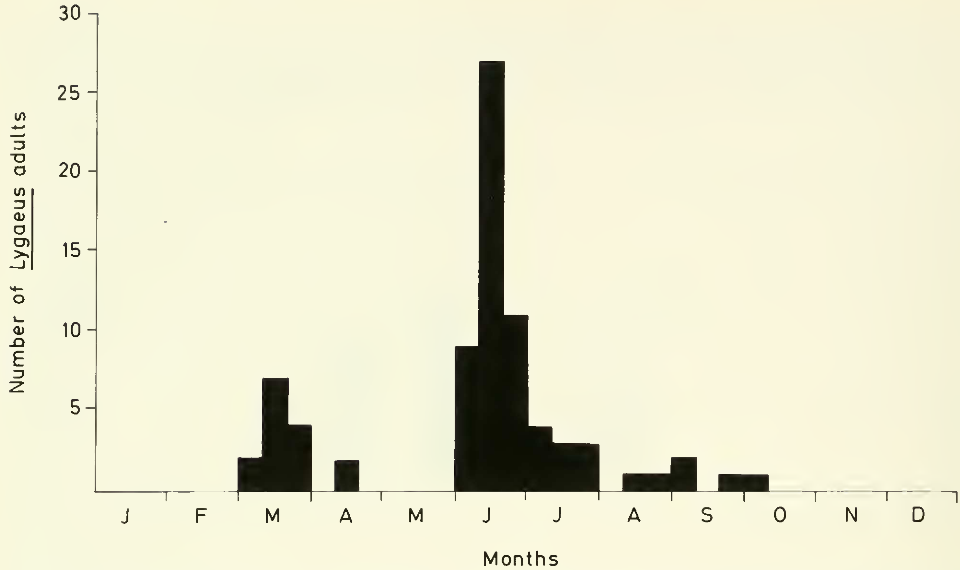

Fig. 4. Collections of adult *L. kalmii* alighting in nine elevated yellow-pan traps that were emptied weekly from January 1976 to December 1982. The bars denote the total numbers captured during the early, middle, and late portion of each month.

From 7 October 1975 through 10 August 1976, Walter Koenig collected the *L. kalmii* that alit in nine "yellow-pan" traps that were widely scattered in the grasslands at the Reservation. The pans, which were a "school-bus yellow" color and contained water and detergent (surface area = 864 cm^2), were attached to posts so that the water level was at least 125 cm above the ground. These collections (Fig. 4) reveal that dispersal during 1976 occurred during the period when the teneral adults of the spring generation normally appear. Furthermore, these data suggest that there are flights in the very early spring, when the adults leave their winter quarters.

I carried out some simple experiments on host-finding behavior in 1975, during the period when the spring generation was dispersing. In each experiment, I stripped the leaves from a few milkweed plants and placed these, together with the chopped up stems, in small enamel trays. On sunny days, these trays were placed out in locations that were at least 100 m away from the nearest milkweed plant. Adults often located these trays within a few hours (Table 2). Since the chopped up plants bore little visual resemblance to a living milkweed, it seems likely that the bugs found the trays by using olfactory cues. On 6 July, I watched as late-arriving individuals approached a tray by flying in from a distance along a straight and level path. Since several bugs were already present at the tray, the possibility remains that such late arrivals were orienting to some cue given off by conspecifics.

Enemies

I saw only one case of predation in the field even though I observed many thousands of insects in the microhabitats utilized by *L. kalmii*. On 10 June 1975, I discovered an adult reduviid, *Rhynocoris ventralis* (Say) det. by J. L. Herring,

Table 2. Arrival of *L. kalmii* at trays containing freshly chopped up milkweed foliage and stems.

Date	Time Tray Set Out	Observations
21 June	1340	9 adults present at 1500
23 June	1300	2 adults present at 1345
6 July	1100	7 adults present at 1330, 5 more arrived the following hour
7 July		
Tray A	1200	No bugs present at either 1400 or 1515
Tray B	1200	4 ♀♀ collected at 1400, 4 new ♀♀ and 4 ♂♂ collected at 1515

feeding on a freshly dead, adult *L. kalmii.* On four occasions, I staged encounters in a cage during which *R. ventralis* adults easily killed vigorous, adult *L. kalmii.* Since two adult *R. ventralis* were maintained from 10 June–14 July on a diet of *L. kalmii,* it is clear that these predators can cope effectively with the cardenolides that the lygaeids contain at this season (Isman et al., 1977). Cannibalism, involving all life stages of *L. kalmii,* appears to be a relatively important cause of mortality (see Food Habits).

The aposematic traits observed in other milkweed bugs, e.g. *Oncopeltus* spp. (Root and Chaplin, 1976), are not so strongly expressed in *L. kalmii.* When suddenly approached or touched, *L. kalmii* adults often drop from vegetation and scurry under the litter or down rodent diggings. While the bugs are somewhat conspicuous when perched on milkweeds, individuals that are against a background of plant debris or broken soil can be easily overlooked.

I reared two parasitoids from ca. 125 field-collected adults and nymphs that were maintained in cages during the spring and early summer. A tachinid fly, *Hyalomya robusta* (Brooks) det. by C. Sabrosky, which had developed in an adult of unknown age, emerged on 26 June 1975. Another tachinid, *Leucostoma gravipes*

Table 3. Densities of major insects on *Asclepias eriocarpa* in Monterey County, California and on *Asclepias curassavica* near Cali, Colombia. All censuses are from samples of the terminal 30 cm from 50 stems. The study area in Colombia is described in Root and Chaplin (1976).

Locality:	California				Colombia				
Census Date:	21 Jun 1975	6 Jul 1975	18 Aug 1976	4 Aug 1983	9 Feb 1971	19 Apr 1971	15 May 1971	12 Jul 1971	5 Aug 1971
Dry weight of plants sampled (g):	498	516	692	ND	112	114	83	159	98
Numbers of:									
Lygaeus kalmii	105	117	37	49	0	0	0	0	0
Lygaeus reclivatus	0	0	0	0	0	0	0	0	1
Oncopeltus cingulifer[1]	0	0	0	0	24	3	2	8	3
O. unifasciatellus[1]	0	0	0	0	4	1	13	14	5
Undet. lygaeid nymphs	0	0	2	0	201	1	3	69	0
Aphis nerii	0	0	0	0	405	344	640	1544	1402
Tetraopes basalis[2]	7	4	0	2	0	0	0	0	0
Chrysochus cobaltinus[3]	1	2	1	6	0	0	0	0	0
Danaus spp. larvae	0	0	1	1	24	9	5	10	1

[1] Lygaeidae, [2] Cerambyciidae, [3] Chrysomelidae.

(Wulp.) det. by C. Sabrosky, which developed in an overwintered adult *L. kalmii,* emerged on 3 July 1975. The rate of parasitism I observed was much less than has been reported in midwestern populations (Simanton and Andre, 1936; Dingle, personal communication).

Relationship to Milkweeds and Their Fauna

Even though *L. kalmii* is polyphagous in the usual sense of the word, it has a special connection with milkweeds. This is reflected in the apparent ability of the adults to orient to milkweed odors, the concentration of adults in milkweed stands during June and July, and the prolonged reproductive diapause during June when milkweed pods are unavailable. The host relationships are thus broadly similar to those of *Lygaeus equestris* in Sweden (Solbreck and Kugelberg, 1972; Kugelberg, 1973, 1974); both species can survive and reproduce while feeding on a wide variety of seeds, but they are strongly associated with an asclepiadaceous host during those seasons when the plants are maturing pods and shedding seeds. They differ in that the Swedish bugs, which experience a relatively contracted and cool growing season, normally exploit a seasonal succession of hosts in completing only a single annual generation. In California, the extended season, coupled with the facultative host requirements of *L. kalmii,* results in at least two generations being produced each year which exploit milkweeds during different stages in their development.

During 1975 and 1976, *L. kalmii* was the most abundant insect on milkweeds in the Coast Range (Table 3, and other observations). The densities of *Lygaeus* spp. measured in Colombia (Table 3) and Illinois (Price and Willson, 1979) are much lower. The match between *L. kalmii* and conditions in the Coast Range tends to foster a heavy impact on milkweeds. As a consequence of its having a facultative diet, the number of adult *L. kalmii* produced by the spring generation depends, to a large extent, on factors that are unrelated to the status of the "preferred" milkweed host. The environment at the Hastings Reservation usually provides an abundance of requisites for this generation; extensive rodent diggings create disturbances where weed seeds abound in close proximity to bare areas used for basking and the normally sunny weather of spring promotes early and rapid development. The adults of this generation emerge when *A. eriocarpa* stands out as a succulent "oasis" in the drying grassland. Here it should be emphasized that *A. eriocarpa* is a long-persisting, summer perennial; thus it lacks the attributes of successional and "non-apparent" plants that have been used to interpret the ecology and evolution of milkweed insects in other regions (e.g. Caldwell, 1974; Price and Willson, 1979).

After the spring adults shift to *A. eriocarpa* in June, *L. kalmii* is capable of producing herbivore loads that are quite high as compared with the loads measured on milkweeds in other temperate zone localities (Table 4); the factors promoting the heavy loads observed in tropical Colombia are discussed in Root and Chaplin (1976). Throughout the early summer of 1975, the density of *L. kalmii* at the Hastings Reservation consistently exceeded two adults per stem and it was often much higher in the smaller milkweed stands (the data reported in Tables 3 and 4 are from the Arnold Field, the most extensive stand in the vicinity). The arrival of these adults in the milkweed stands several weeks before the seeds become available serves to further increase their impact. Their intense feeding on the

Table 4. Herbivore loads on milkweeds at several localities in North and South America. The loads are expressed as the mg (dry wt) of herbivores (excluding nectarvores) per 100 g (dry wt) of plant material. The data come from samples of the terminal 30 cm from 50 stems growing in large milkweed stands.

Locality	Host	Sample Date	Plant Phenology		Herbivore Load (mg/100 g)
			Flowers	Pods	
California	*A. eriocarpa*	21 June	+	O	277.5
		6 July	+	O	428.6
		18 Aug	+	+	38.4[1]
Colorado	*A. speciosa*	8 Aug	+	+	110.7
		9 Aug	+	+	70.5
Missouri	*A. syriaca*	17 Aug	O	+	36.5
		18 Aug	O	+	50.3
New York	*A. syriaca*	26 July	+	+	4.3
		30 July	+	+	32.5
		7 Sept	O	+	42.4
Colombia	*A. curassavica*	9 Feb	+	+	559.3
		19 Apr	+	+	303.9
		15 May	+	+	312.3
		10 July	+	+	505.2
		5 Aug	+	+	292.5

[1] Samples taken on a day of unseasonable rain and cold.
All other samples in the table were taken on clear, warm days during the late morning.

plants' reproductive tissues causes many flowers to wither prematurely and probably accounts for the complete failure of the pod crop in several small stands during 1975 and 1976. Furthermore, these voracious adults feed heavily on the inactive and sluggish stages of other insects. Since *L. kalmii* can utilize milkweeds containing cardenolides that are toxic to many other animals, it is not surprising that the adults readily attack other milkweed herbivores that sequester these compounds (see list in Rothschild, 1973), such as *Danaus plexippus* at the Reservation and *Oncopeltus fasciatus* in the eastern United States (Ralph, 1977). This combination of great abundance, omnivorous habit, and indifference to cardenolides makes *L. kalmii* a potentially serious threat to any milkweed insect that must pass through vulnerable life stages during July and August. In this regard, it is interesting that *D. plexippus* was relatively rare at the Hastings Reservation during my investigation (Table 3 and other observations) even though its famous overwintering sites at Pacific Grove, California, are nearby and that *O. fasciatus* has never been observed at the Reservation even though abundant populations occur elsewhere in California (K. Evans, personal communication). The possibility that *L. kalmii* can limit the populations of milkweed specialists has several interesting implications that warrant further investigation.

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